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The Identity of *Sciurus duida* J. A. Allen (Rodentia: Sciuridae)

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ABSTRACT

The holotype of *Sciurus duida* is shown to be a composite: the skull is a subadult *Sciurus spadiceus* of unknown provenance, the skin a mature

specimen of *Sciurus igniventris* from southern Venezuela. The name *duida* is restricted to the skin.

INTRODUCTION

I report here the mismatch of skin and skull in the type specimen of *Sciurus duida* J. A. Allen (1914). The composite was discovered in the process of preparing the revision of Catalogue of Type Specimens of Recent Mammals in the American Museum of Natural History (Goodwin, 1953). Describing the error, identifying the species represented by each element, and formally tying the scientific name to the skin will establish the morphological limits the name designates. This action is important because the name is available to revisers for a taxon that may have biological meaning within the group of South American giant squirrels.

Systematic revision of the native South American sciurids in general and of the giant

squirrels in particular is needed. South American tree squirrels are thought to comprise 3 genera: *Sciurillus*, *Microsciurus*, and *Sciurus*, and to contain 15 species according to the compilation, Mammal Species of the World (Honacki et al., 1982). This compilation lists 1 species of *Sciurillus*, a possible 4 South American species of *Microsciurus*, and 11 species of South American *Sciurus*. The most recent revision of the genus *Sciurus*, however, is J. A. Allen's Review of the Sciuridae (1915).

Recent taxonomists have studied the relationships of one or two South American squirrel species in a circumscribed geographic region. Hershkovitz (1947) reviewed *S. granatensis* of northern Colombia and northwestern Venezuela and established morpho-

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logical distinctions between the giant squirrel species *S. spadiceus* Olfers and *S. igniventris* Wagner. Patton (1984) clarified the relationship between the two species in the western Amazon Basin. Moore (1959), reporting on the relationships of the living Sciurinae, was primarily concerned with suprageneric characters and classification. Cabrera's checklist of South American mammals (1961) included the genus *Sciurus*, but did not include or comment on Hershkovitz's (1959) report.

Series of South American squirrels are well represented in collections in the United States and Europe, but a major problem for anyone revising South American *Sciurus* is the proliferation of scientific names. Those associated with *S. igniventris* include: *versicolor*, *zamorae*, *steinbachi*, *cocalis*, *duida*, *fulminatus*, *manhanensis*, and *taedifer*, while some of those associated with *S. spadiceus* are: *langsdorffii*, *pyrrhonotus*, *tricolor*, *morio*, *fumigatus*, *bruneoniger*, *castus*, *nigratus*, *variabilis*, *rondoniae*, *urucumus*, *steinbachi*, *juralis*, *taparius*, and *purusianus*. The validity of these names or the relationships of the animals to which they are assigned is not at all clear throughout the geographic range of these squirrels.

This report establishes the limits of one name assigned to the South American giant squirrels.

METHODS AND MATERIALS

All of the specimens examined and discussed are in the collections of the Department of Mammalogy at the American Museum of Natural History (AMNH). Measurements were taken with a dial caliper accurate to 0.05 mm. The skull measurements are standard but the following procedures should be noted. Nasal length was taken as length of suture between nasal bones. Rostral length was taken on the dorsal surface of the skull from the anteriormost point of the internasal suture to the junction of the maxillary and the premaxillary. Temporal breadth was taken at the supraorbital notch. Least interorbital was measured at the narrowest point posterior to the orbital processes.

Materials:

Sciurus igniventris

Venezuela: Amazonas; Mt. Duida

Playa del Rio Base: AMNH 77356, 77357
 Pié del Cerro: AMNH 77358
 Savana Grande: AMNH 77359, 77360
 Foothills Camp: AMNH 77361
 Rio Pescado: AMNH 77362, 77363, 77364
 Rio Cunucumá: AMNH 36152, 36153 (holotype of *Sciurus duida*), 36154
 Venezuela: Amazonas; Rio Orinoco
 Boca Rio Ocame: AMNH 78003, 78004
 Casiquiare: AMNH 78005, 78006, 78008, 78009, 78010

Sciurus spadiceus

Brazil: Amazonas; Rio Amazonas south bank, Villa Imperatriz
 Santa Clara: AMNH 93033, 93035, 93036, 93037, 93038
 Boca Lago Teffé: AMNH 78947
 Lago Teffé, Santa Isadora: AMNH 78948
 Boca Rio Andira: AMNH 93551
 Brazil: Pará; Rio Tapajoz
 Igarapé Amorin: AMNH 95746, 95748
 Brazil: Amazonas; Rio Madeira
 Auará Igarapé: AMNH 91818
 Rosarinho, Lago Sampaio: AMNH 92749, 92754, 92757
 Peru: Loreto; Rio Napo
 Boca Rio Curaray: AMNH 72229, 72227, 72226
 Boca del Lagarto Cocha: AMNH 72233, 72237, 72238, 72240

All specimens of *Sciurus igniventris* are adult skins and skulls except AMNH 36152, 36154, 77365, 77364, which are skins only. Those of *Sciurus spadiceus* are skulls and skins at different stages of molting from juvenile to adult pelage. The Brazilian localities are those nearest to Mt. Duida.

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PROBLEM AND SOLUTION

J. A. Allen exemplified some of the difficulties encountered by his generation of taxonomists in the section titled General Considerations (pp. 158–169) in his Review of the South American Sciuridae (1915). Allen evaluated the customary characters to consider when making a taxonomic assessment: premolar formula, mammae, size, pelage and coloration, and skull and teeth. He sensed

that the consistent presence or absence of the third upper premolar is of "genetic importance" but could not develop a phylogenetic hypothesis based on this character. He recognized number of mammae as being consistent within groups of squirrels, but he was not clear at what taxonomic level it was important.

Consideration of body size raised the problems of measurement. He recognized that he did not have a standard for which measurements to take or how to take them, but understood that a consistent standard was needed. As cranial measurements are difficult to make, he decided that they were of little value. For the measurements that he could make with assurance (tail length and total length), he considered the average for 10 specimens more reliable than that of a single specimen. Writing about 20 years before the population concept entered biology, Allen viewed averaging a series as a means of controlling variation. He considered pelage texture of taxonomic value only for distinguishing subspecies. Pelage color he regarded as a trustworthy index of genetic relationship and in the South American squirrels as an indication of group affinity.

Allen asserted that dorsal contour of skull varies with age and in animals of the same age; that rostrum and interorbital breadth vary with age; and that crown patterns of fourth upper premolar, third upper molar and, to a lesser extent, first and second upper molars are not consistent. However, he had not sorted out the precise variation due to age, sex, or wear of tooth crowns. The limits of Allen's knowledge and his consequent assumptions account for the history of his naming *S. duida*.

In November 1912, Leo Miller led an American Museum expedition to the Upper Orinoco in southern Venezuela to collect birds and mammals on Mt. Duida at elevations between 3500 and 4000 ft. Miller and his assistant reached San Fernando de Arabapo on February 2, 1913, and the junction of the Rio Orinoco and the Rio Cunucunumá in mid-March. After traveling about 18 mi up the Cunucunumá to Boca Sina, Miller was forced to turn back because his assistant had become ill with beri-beri. They had collected approximately 400 specimens.

In a confidential letter to Frank Chapman



Fig. 1. *Sciurus duida*, ventral view of study skin.

TABLE 1
Characters Separating *S. spadiceus* and
S. igniventris, in Hershkovitz, 1959

<i>spadiceus</i>	<i>igniventris</i>
1. Skull long, relatively narrow with flattened dorsal contour.	1. Skull relatively broad with rounded dorsal contour.
2. Muzzle elongate.	2. Muzzle moderately long.
3. Well developed temporal ridges converge posteriorly to form single crest on well defined interparietal.	3. Moderately developed temporal ridges are separated on interparietal.
4. Condyllobasal length in adults over 59 mm.	4. Condyllobasal length less than 63 mm in adults.
5. Braincase width at parietals 30–43% of condyllobasal length.	5. Braincase across parietals 43–48% of condyllobasal length.
6. Temporal ridge breadth at frontoparietal suture 15–26% of condyllobasal length.	6. Temporal ridge breadth at frontoparietal suture 24–34% of condyllobasal length.
7. Sphenopalatine fissure enlarged 1½ times diameter of optic foramen.	7. Sphenopalatine fissure small or obsolete.
8. Lower incisor long. Chord of exposed tooth rarely shorter than condylar process height from mandible base.	8. Lower incisor normal. Chord of exposed part always shorter than condylar process height from mandible base.
9. Upper surface of feet always as dark or darker than shoulder and thighs—black or mixed reddish black.	9. Upper surface of feet lighter or paler than shoulders and thighs—ochraceous to reddish orange.
10. Crown black or with well defined black cap.	10. Crown usually ochraceous or orange without dark cap.
11. Postauricular tufts not well defined when present.	11. Bright postauricular tufts always present.
12. No black lateral lines defining sides from venter.	12. Black lateral lines defining sides from venter often present.

dated May 19, 1913, Miller emphasized that throughout the trip fresh produce had been plentiful and fresh meat available from the squirrels they had collected. Later that same month, Miller reported to Chapman that the specimens collected on the Mt. Duida trip

TABLE 2
Characters Separating *S. spadiceus* and
S. igniventris in Patton, 1984

<i>spadiceus</i>	<i>igniventris</i>
1. Absolutely longer in rostral region and mandible.	1. Smaller skull, shorter, broader muzzle.
2. Relatively narrower interorbital region especially behind postorbital processes.	2. Relatively broader interorbital region especially anterior braincase just behind postorbital process.
3. Palatal width at M1 narrower than <i>igniventris</i> .	3. Palatal width at M1 greater than <i>spadiceus</i> .
4. Width of mesopterygoid fossa smaller than in <i>igniventris</i> .	4. Width of mesopterygoid fossa greater than in <i>spadiceus</i> .
5. Masticatory foramen more posterior on alisphenoid than in <i>igniventris</i> .	5. Masticatory foramen adjacent to anterior margin of alisphenoid.
6. Foramen ovale and foramen accessorius larger.	6. F. ovale and f. accessorius smaller than in <i>spadiceus</i> .
7. Moderate sphenopalatine vacuities.	7. Sphenopalatine vacuity usually absent.
8. Gets smaller on north-to-south cline; southern populations approach <i>igniventris</i> in size.	8. Little variation on north-to-south cline.
9. Maxillary root wider.	9. Maxillary root narrower.
10. Bony orbits smaller between supraorbital flange and zygomatic arch.	10. Bony orbits larger between supraorbital flange and zygomatic arch.
11. Dorsal surface of hind feet orange-red grizzled with black.	11. Dorsal surface of hind feet orange red.

had been carefully packed and would be held at Peninsula de Paria (northeastern Venezuela due west of Port of Spain, Trinidad) until a collection had been made there, then all would be shipped to New York. The collection arrived at the American Museum on July 8, 1913.

Allen (1914) described *Sciurus duida*, holotype AMNH 36153, based on three skins from Rio Cunucunumá and an unlabeled skull from the Miller Mt. Duida Expedition. In a footnote to this paper (p. 594), Allen wrote:

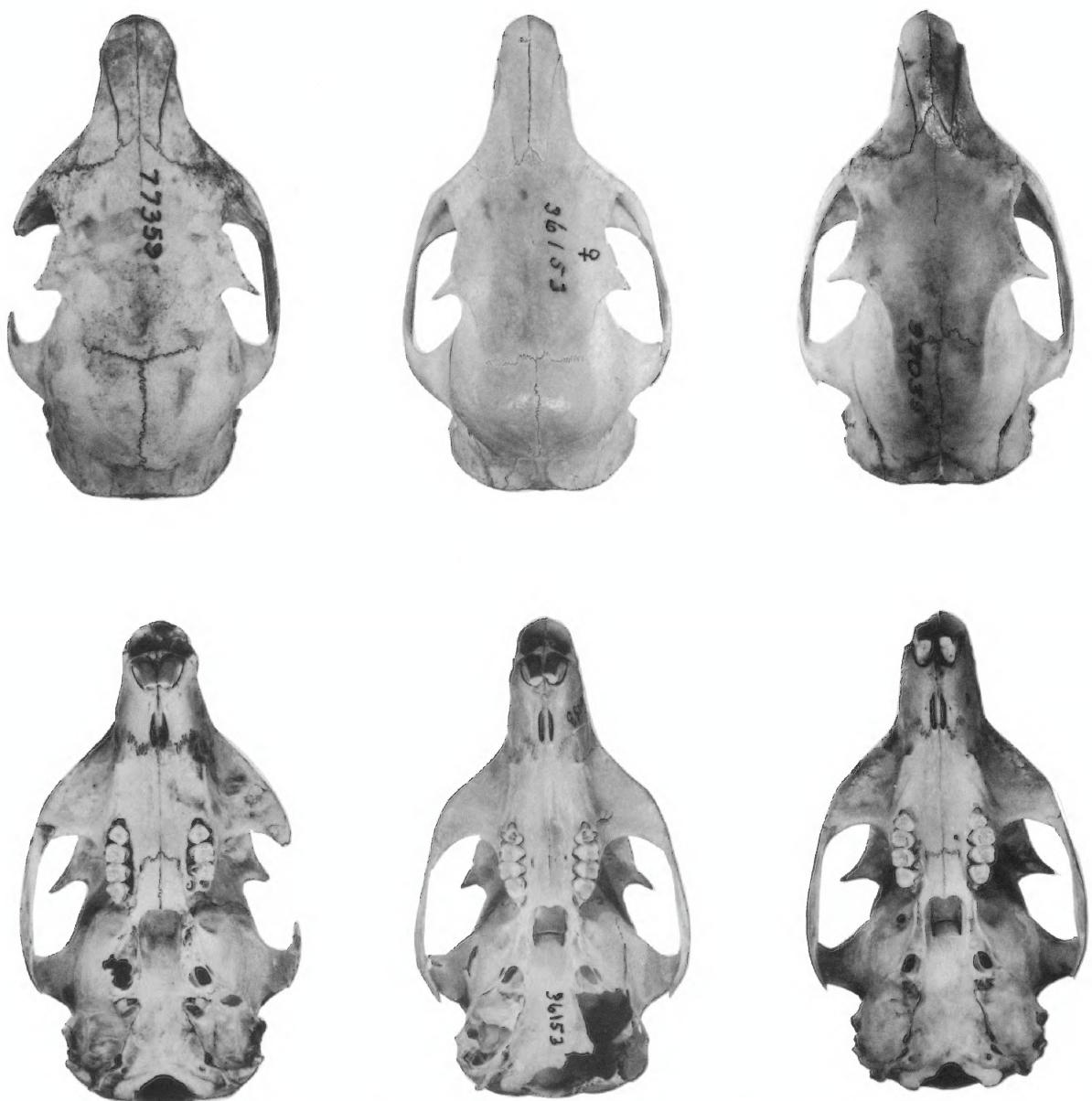


Fig. 2. Crania of South American giant squirrels. Dorsal view above. Ventral view below. **Left:** AMNH 77359, *Sciurus igniventris* from Savana Grande, Venezuela. **Center:** AMNH 36153. **Right:** AMNH 93035, *Sciurus spadiceus* from Villa Bella Imperatiz, Amazonas, Brazil. Natural size.

The collector's number on the skull unfortunately was lost, but by exclusion it must have belonged to one of the three skins of this species, and almost beyond doubt to the one selected as type, the other two being young adults, while this is fully adult, like the type skin.

In the body of the diagnosis, Allen observed that:

In form the skull of *Sciurus duida* most nearly resembles *S. tricolor*, especially in the narrow, slender, and relatively long rostrum, but it has no resemblance to that species in the coloration or texture of pelage, in which it most resembles the *igniventris* group, with which, however, the form of the skull denotes no close relationship.

Sciurus duida was problematic from its origin. Tate (1939) placed it as a subspecies of



Fig. 3. Crania of South American giant squirrels. Left lateral view. **Top:** AMNH 77359, *Sciurus igniventris* from Savana Grande, Venezuela. **Center:** AMNH 36153. **Bottom:** AMNH 93035, *Sciurus spadiceus* from Villa Bella Imperatriz, Amazonas, Brazil. Natural size.

S. igniventris and was of the opinion that only pelage color separated *S. duida* from *S. igniventris*. He made no comment about the skull characters Allen had mentioned or about Allen's footnote. When Goodwin compiled his catalog, he followed Tate and listed *S. duida* as a subspecies of *S. igniventris* (Goodwin, 1953).

I examined the holotype of *Sciurus duida* in the course of preparing a revision of Goodwin's catalog of American Museum mammal types. The skin, shown in figure 1, is that of a large, mature female with prominent mammae. The skull, though large, is that of an immature squirrel: cranial sutures open or

only peripherally fused; fourth upper premolar erupted to the level of first upper molar and with slight wear on occlusal surfaces of cheekteeth. Dentine is not visible on the cusps of any of the cheekteeth. When compared with South American giant squirrels in the AMNH collection, the degree of development and tooth wear of the type skull matched that of the South American giant squirrels that had not completed molt to adult pelage.

Hershkovitz (1959) and Patton (1984), the most recent to study these squirrels, agree that there are two species of South American giant squirrel, *Sciurus spadiceus* Olfers, 1818, and *Sciurus igniventris* Wagner, 1842. They also agree on three characters that separate the two species: muzzle length and shape, size of sphenopalatine vacuities, and color of the dorsal surface of the hind feet. Each author presents a further suite of characters that distinguishes the two species (tables 1 and 2).

The cranium of AMNH 36153, shown in figures 2 and 3, agrees with characters given by both Hershkovitz and Patton for *Sciurus spadiceus*. The skull is that of a young adult squirrel and lacks the mandible. It has an elongated muzzle, flattened dorsal contour, and temporal ridges that converge posteriorly to cross the interparietals in close parallel. The sphenopalatine vacuities are large as are the foramina ovale and accessorius. Measurements are listed in table 3. Immaturity accounts for the temporal ridges not quite meeting over the interparietals and for the measurements and proportions being slightly different from those cited by Hershkovitz and Patton for *Sciurus spadiceus*.

The skin assigned to the skull by J. A. Allen is that of a sexually mature, probably multiparous *Sciurus igniventris* female. It has orange-red hind feet grizzled with black and are paler than the shoulders and thighs. The crown is grizzled, darker than the rest of the dorsal pelage, but lacks a defined cap. Pale postauricular tufts are present. Patton gives only one pelage character, that of hind feet grizzled with black for *S. spadiceus*, and clear orange or orange red for *igniventris*. However, this clear color does not hold for *S. igniventris* in Venezuela.

In a series of 19 *S. igniventris* specimens from Venezuela in the AMNH collection, 7 have hind feet grizzled with black. All, griz-

TABLE 3
Cranial Measurements (in millimeters) of Holotype AMNH 36153, *S. spadiceus* from
Northwestern Brazil, and *S. igniventris* from Southern Venezuela^a

	#36153	<i>S. spadiceus</i>	<i>S. igniventris</i>
Greatest length	65.8	65.3 ± 1.10 (63.1–67.1) 12	64.3 ± 1.50 (61.2–67.0) 9
Condylarbasal length	55.7	55.9 ± 1.20 (53.1–58) 14	53.7 ± 1.90 (50.5–57.4) 11
Rostral length	21.6	19.2 ± 0.70 (17.8–20.3) 12	18.8 ± 1.10 (17.3–20.8) 12
Nasal length	19.8	16.7 ± 1.30 (14.2–18.8) 12	18.6 ± 1.30 (16.3–21.2) 12
Diastema length	19.4	19.2 ± 0.70 (18.4–20.3) 14	17.9 ± 0.79 (16.5–19.6) 14
Maxillary tooth row length	10.0	10.5 ± 0.52 (9.9–11.7) 12	10.7 ± 0.51 (9.9–11.7) 14
Least interorbital	19.6	19.7 ± 0.63 (18.6–20.4) 14	21.3 ± 0.39 (20.6–22.0) 13
Temporal breadth	20.1	21.0 ± 0.71 (19.5–22.1) 14	19.2 ± 2.20 (16.3–22.0) 14
Palatal width at M1	6.5	7.3 ± 0.59 (6.0–8.5) 14	7.5 ± 0.25 (7.0–7.9) 13
Braincase width	25.1	24.5 ± 1.10 (22.3–27.5) 14	26.4 ± 0.53 (26.1–27.2) 11
Optic foramen	3.2	2.8 ± 0.23 (2.3–3.1) 14	2.6 ± 0.54 (1.5–3.0) 12
Foramen ovale	2.6	2.5 ± 0.36 (2.0–3.1) 14	2.7 ± 0.28 (2.3–3.1) 11
Foramen accessorius	1.3	1.8 ± 0.26 (1.3–2.1) 14	1.5 ± 0.29 (2.3–3.1) 11
Sphenopalatine vacuity	4.3	4.6 ± 0.70 (3.2–5.7) 13	Not measurable

^a Mean ± 1 standard deviation, observed range (in parentheses), and number of specimens.

zled or not, have feet paler than thigh and shoulders and dark crowns without a well defined dark cap like AMNH 36153. All also have pale postauricular tufts. Only two of the series, the paratypes of *Sciurus duida*, AMNH 36152 and AMNH 36154, are skins without skulls.

The eight specimens of the collection found by the Olalla brothers in 1928–29 at the foot of Mt. Duida are almost indistinguishable from the three skins Miller collected in 1913. All 19 specimens agree with Hershkovitz's characters for the hind feet and postauricular tufts. The series does not agree with his description of the crown as orange and ochraceous, but does agree in lacking a defined cap. None of the specimens in this series has a black lateral line between side and venter, which Hershkovitz found was often present. However, the 16 available skulls do have the *S. igniventris* characters of shortened rostra, tiny or absent sphenopalatine vacuities, small foramina ovale and accessorius, and skull proportions within the range given by Hershkovitz (table 1).

Sciurus duida J. A. Allen 1914 is based on the mismatch of a young adult skull of *Sciurus spadiceus* Olfers 1818 and the skin of a mature *Sciurus igniventris* Wagner 1844. Allen erred in equating the age of the unlabeled squirrel skull with that of the skin from Rio Cunucunumá. It is likely that the carcasses

of the skins from Rio Cunucunumá were used for food. The provenance of the unlabeled skull is not known and cannot be traced. The skin was labeled in the field by the collector, Leo Miller, leaving no doubt as to its provenance. I therefore restrict the name *duida* to the skin from Rio Cunucunumá. The name is now available for the southern Venezuelan population of *Sciurus igniventris* if it is found to be a distinct taxon.

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